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The Biological Klepton Concept (BKC)[*]

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The proposal of DUBOIS & GÜNTHER (1982) to create a new systematic
category (klepton) embracing the hybridogenetic and gynogenetic taxa (sensu
lineages, genealogies) is analyzed. Such taxa can be considered neither as
simple hybrids nor as good species.

Biological trends for all known kleptons in the *Ambystoma*, *Rana*,
Phoxinus, *Poecilia* and *Poeciliopsis* complexes are summarized, and their new
associated terms discussed.

Kleptons are historical entities, but not of the classical Biological Species
Concept (BCS sensu MAYR, 1982), but showing equally ecological, genetical,
and evolutionary relevances as their associated "good" species.

From an epistemological point of view, the fact that so-called kleptons
are not subject to cladistic laws (because kleptons are polyphyletic), must not
be considered as and argument for ignoring the existence of those taxa, either
biologically or taxonomically.

Klepton evolutionary rules, as parallel species pathways, are discussed:
we conclude that not all evolutionary processes take place in the species
context.

The Biological Klepton Concept (BKC) is proposed: a klepton is a
community of populations with a hybrid genome derived from the same
parental species, reproductively dependent upon sympatric species that play
the rôle of sexual host.

" But what about viruses ? Can they be classified in Linnean fashion ? (...) The only
attribute of life possessed by viruses is reproduction with genetic continuity and the
possibility of mutation. Evolution can therefore occur. " (GOODHEART, 1969. 38).

NATURAL TAXA MUST BE NAMED

I suppose all evolutionary biologists agree with this statement, in spite of rare biological characteristics or atypical reproductive modes in taxa of certain lineages. The example of viruses is very clear: we don't know if it can be said that viruses are alive (they have no intrinsic metabolism), but viruses do have names because they constitute historical entities (acting as genetical cell parasites of animals and plants), and names are needed to facilitate studies on them.

Parthenogenetic, gynogenetic, and hybridogenetic populations constitute special taxa in the Animal Kingdom. Briefly it can be said that parthenogenetic unisexual females reproduce without sperm, whereas gynogenetic unisexual females need sperm of associated species for reproducing, the genome of which is not included into the egg after fertilization; finally, hybridogenetic taxa need either the sperm or the ovocytes of associated species for reproducing, the genome of which is incorporated into the egg. The analogy with respect to viruses is clear: as viruses are genetic parasites of cells (the biological unit, MAYR, 1982), thus gynogens and hybridogens are genetic parasites of " good " species (the unit of evolution, MAYR, 1982).

Nomenclature of parthenogenetic, gynogenetic, and hybridogenetic taxa is a systematic topic currently of major interest, due to biological paradoxes in those populations which put in question the classical concept of species. Discussions at the Ann Arbor meeting made evident that:

(1) Parthenogenetic population must be named and considered separately from gynogenetic and hybridogenetic populations.

(2) Parthenogenetic populations are genetically autonomous, constituting taxa with clonal genetic inheritance, and frequently with hybrid origin as their primary speciation event (see discussions in CUELLAR, 1987). Parthenogenetic reproduction is asexual (sensu MAYNARD SMITH, 1986) and automitic (sensu MOGIE, 1986).

(3) Gynogenetic and hybridogenetic populations do not constitute genetically autonomous taxa. They reproduce sexually, with well-established mechanisms of mating choice (see for instance BLANKENHORN, 1977; KEEGAN-ROGERS & SCHULTZ, 1988)

(4) Gynogenetic and hybridogenetic populations cannot be included in the Biological Species Concept (BSC, sensu MAYR, 1942, 1982).

It is my wish to consider in this paper only nomenclatural treatment for gynogenetic and hybridogenetic taxa. Biological characteristics concerning reproductive modes, gametogenetic mechanisms, hybrid genome composition, ploidy, and sexual parasitism, for different gynogenetic and hybridogenetic taxa are reviewed and summarized as they occur in fishes and amphibians.

Major controversies concerning nomenclatural treatment of gynogenetic and hybridogenetic taxa have originated from ambiguous discussions on their conformance (or not) with the unitary concept of species. I here show that the biological characteristics of those taxa are quite unitary, but far different from those of the BSC. Accordingly, I propose

herein a Biological Klepton Concept (alternative to BSC). Kleptons are regarded as distinct, natural, and real biological entities, extrapolating from the term and systematic category created by DUBOIS & GÜNTHER (1982).

THE DEFINITION OF KLEPTON
GIVEN BY DUBOIS & GÜNTHER (1982)

The aim of these two authors was " ..to provide a general name and nomenclatural rules for some particular animal ' forms ' which cannot be properly considered as ' biological ' species, such as gynogenetic and hybridogenetic unisexual fish of the genus *Poeciliopsis*, gynogenetic unisexual fish of the genus *Poecilia*, gynogenetic unisexual salamanders of the genus *Ambystoma*, and hybridogenetic (or leaky hybridogenetic) frogs of the genus *Rana*. All these forms, despite their diversity, have the following features in common: they are of hybrid origin; their heredity is clonal or hemiclonal; for their reproduction such forms depend on the gametes of a distinct ' good ' species. " (DUBOIS & GÜNTHER, 1982: 290).

From a practical point of view, creation of the new term *klepton* provides simplicity, ready dichotomy, university of application and a precedent for naming further, still unknown categories of taxa.

From an evolutionary point of view, the term klepton excludes the Biological Species Concept, and connotes a new one, the Biological Klepton Concept.

From a genetical, ecological, and ethological point of view, the term klepton implies the hybrid genetic character of its taxa, as well as their reproductive modes that involve a genetical parasitism of hybrids on their " good " associated parental species. Special mate choice ethograms and ecological niches are involved in the klepton concept.

All of these biological characteristics are entailed in use of the term klepton, which nomenclaturally can just be introduced as an abbreviation between the binomial terms, i.e.: *Rana* kl. *esculenta*, *Poecilia* kl. *formosa*.

KLEPTONS ARE NOT SPECIES

" Species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other groups. " (MAYR, 1942: 120).

" An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies. " (SIMPSON, 1961: 153).

" A species is a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature. " (MAYR, 1982: 273).

To my knowledge, Ernst MAYR never considered specifically in his works the cases of hybridogenetic and gynogenetic populations. In fact findings concerning these taxa are very recent and their biological interest remains still ignored in general zoological books.

However, the father of the BSC clearly separated parthenogenetic taxa from parameters of the unitary species: " The biological species concept is based on the reproductive isolation of populations. The concept, therefore, cannot be applied in groups of animals and plants that have abandoned bisexual reproduction. " (MAYR, 1982. 283).

In contrast to MAYR, several authors (as FROST & WRIGHT, 1988) have proposed solutions for naming parthenogenetic taxa, considering them as species, from cladistic points of view: " ... a lineage concept, later redefined by WILEY (1978) as the largest monophyletic group whose components are not irretrievably on different phylogenetic trajectories ". Reading WILEY (1978), however, one concludes that FROST & WRIGHT (1988) merely present an interpretation of WILEY's evolutionary concept of species (modified from SIMPSON, 1961), not of anatomically unisexual taxa.

The systematic protocol for hybridogenetic and gynogenetic populations thus remains indeterminate. Those taxa are neither asexual as parthenogens, nor reproductively isolated bisexual populations as species. Nevertheless, it is true that some gynogenetic populations reproduce clonally, in analogy to parthenogens. But gynogenetic populations cannot reproduce alone and reproductive isolation is the major biological requirement of autonomous population taxa The point of major importance in classification is the mode of reproduction (that is, genetic parasitism common to hybridogens and gynogens), not the mode of conservation of the genotypes (clonal as in gynogens and parthenogens, hemiclonal or clonal in hybridogens)

BIOLOGICAL CHARACTERISTICS IN KLEPTONS

Kleptons are real entities.

Biological trends in all known gynogenetic and hybridogenetic vertebrate hybrid taxa are summarized in Table I, showing clear analogies between various fish and amphibian complexes. Some very interesting findings concerning " before meiosis ", " pre-meiotic ", and " ameiotic " cytogenetic events, for different complexes, are of major cytological and evolutionary interest These phenomena could be interpreted as convergent solutions to hybridity (from a darwinian point of view), or as a result of neutral mutations in ancestors, before hybridization, well utilized after casual hybridization by gynogens and hybridogens for their reproduction (random walk evolution of the parental species genome, sensu KING & JUKES, 1969, followed by natural selection on hybrids, sensu DOBZHANSKY, 1937).

It is worth noticing that constant presence of some parental genomes have been found in all complexes (the genome " laterale " in Ambystoma kleptons, as well as the presence of the genome "ridibunda " in all Rana kleptons, or the presence of the genome " monacha " in all Poeciliopsis kleptons).

In all cases, the presence of a sexual host associated with each klepton is a clear and distinct fact for all these hybrid taxa.

However, no gynogenetic or hybridogenetic taxa have yet been found in reptiles, where are least 30 parthenogenetic lizard taxa exist (CUELLAR 1987).

Another meaningful reason for considering a common nomenclatural treatment for gynogens and hybridogens is that the *Poeciliopsis* complex includes both hybridogenetic and gynogenetic taxa (see Table I). Likewise it appears (as inferred from the results of BOGART et al., 1987) that gynogenetic and hybridogenetic reproductive modes occur in the very same hybrid individuals, in some populations of *Ambystoma*.

A NEW, MORE GENERALIZED DEFINITION OF KLEPTON : THE BIOLOGICAL KLEPTON CONCEPT (BKC)

The definition of klepton given by DUBOIS & GÜNTHER (1982) was based on three conditions that do not always take place in all hybridogenetic and gynogenetic hybrid taxa. For instance recombinant gametes occur in low frequencies in some rare *Rana* kl. *esculenta* hybridogenetic populations, as well as diploid gametes containing both parental genomes (GRAF & POLLS PELAZ, 1989). In these cases the original definition of klepton would not apply.

Thus I propose a more extensive Biological Klepton Concept: " A klepton is a community of populations with a hybrid genome derived from the same parental species, reproductively dependent upon sympatric species that play the role of sexual host ". An equivalent definition would be: " A klepton is an evolutionary systematic category (parallel to the species pathway) including hybrid populations reproducing by hybridogenesis and gynogenesis ".

I nevertheless agree completely with MAYR (1982) in considering the species as the unit of evolution, as well as the cell is the functional biological unit of life. The analogy of viruses and kleptons, stated previously, reminds how carefully the evolutionary relevance of both groups must be considered, especially of retroviruses and allopolyploid kleptons.

NAMED, AND STILL UNNAMED KLEPTONS

" I don't like to see descriptions of the Evolution as the mean of survival and multiplication of DNA. (...) It would be as absurd as to propose explanations of Eastern literature as the means of survival of the points on the letter i. " (translated from MARGALEF, 1980. 93).

Kleptons could be named in the same way as viruses, using combined numbers or letters referring to their prevailing genomes (transmitted clonally, hemiclonally, or recombined). But kleptons are animals, they are clearly alive, and they have phenotypes analogous to those of the " good " species described by LINNAEUS

In fact one of the reasons prompting DUBOIS & GÜNTHER (1982) to propose the new term klepton was the fact that binomials at the Linnaean fashion already exist for many of those taxa. That is, some kleptons were named as species, and their morphological description and names were available before the discovery of their hybrid character and

Table I. Biological trends for some gynogenetic and hybrid genetic taxa. Major papers and reviews concerning each topic are referred to by numbers:

(1) SCHULTZ (1969) ; (2) FERRIS (1984) , (3) VRIJENHOEK (1984) ; (4) CIMINO (1972a) ; (5) CIMINO (1972b) ; (6) SCHULTZ (1977) ; (7) MOORE (1984) , (8) HUBBS & HUBBS (1932) , (9) RASCH et al. (1982) , (10) MONACO et al (1984) , (11) DAWLEY et al. (1987) , (12) DAWLEY & GODDARD (1988) ; (13) GODDARD et al (1989) , (14) BERGER (1977) , (15) GRAF & MÜLLER (1979) , (16) HEPPICH et al (1982) , (17) POLLS PELAZ (1991) , (18) TUNNER (1974) , (19) GRAF & POLLS PELAZ (1989) , (20) GRAF et al. (1977) , (21) UZZELL & HOTZ (1979) ; (22) UZZELL (1964) , (23) MASLIN (1968) , (24) LOWCOCK et al (1987) , (25) KRAUS (1985) , (26) BOGART et al (1989) , (27) UZZELL & GOLDBLATT (1967) , (28) SERVAGE (1979) , (29) UZZELL (1970) , (30) MACGREGOR & UZZELL (1964) , (31) CUELLAR (1976) , (32) DOWNS (1978) , (33) UZZELL & GOLDBLATT (1967) , (34) LYNCH (1984) , (35) UZZELL (1969) , (36) MORRIS & BRANDON (1984) , (37) BOGART et al (1985) , (38) BOGART & LICHT (1986) ; (39) MORRIS (1985)

Kleptic nomenclature		Parental genome	Gametogenesis	Reproduction mode	Sexual host
Fishes: *Poeciliopsis* complexes					
Precedent nomenclature: hyphenated names₁					
Poeciliopsis kl *monachalucida* Schultz, 1969₂	2n	mon , luc₃	Premeiotic exclusion₄,₅	Hybridogenesis₃,₁,₆	*P lucida*₃,₆
	3n		Endomitosis₄,₅	Gynogenesis₃,₁,₆	*P. lucida, P. monacha*₃,₆
Poeciliopsis kl. *monachaoccidentalis* Schultz,1971₂	2n	mon , occid ₃	Prem exclusion₄,₅	Hybridogenesis₃,₆	*P occidentalis*₃,₆
Poeciliopsis kl *monachalatidens* Schultz,1971₂	2n	mon , latid ₃	Prem exclusion₄	Hybridogenesis₃,₆	*P latidens*₃,₆
Unnamed *Poeciliopsis* klepton	2n	(mon -vir) , luc ₃	Prem exclusion ⁹	Hybridogenesis₃,₇,₆	*P lucida* ⁷,₆,₇
Unnamed *Poeciliopsis* klepton	3n	mon , vir , luc ₃	Endomitosis ⁹	Gynogenesis₃,₆	*P viriosa*₃,₆
Fishes: *Poecilia* complex					
Poecilia kl. *formosa* (Girard, 1859)₂	2n	mex , latip ₄	Apomixis₉,₁₀	Gynogenesis₁₀	*P. mexicana*₁₀
	3n				*P. latidens*₁₀
Fishes: *Phoxinus* complexes					
Unnamed *Phoxinus* klepton	2n	eos, neogaeus₁₁,₁₂,₁₃	(?)	Gynogenesis₁ ₁₂	*P. eos*
	3n			Hybridogenesis ⁹₇,₁₂,₁₃	*P. eos, P. neogaeus*

Amphibians: *Rana* complexes					
Precedent nomenclature. formal names[2]					
Rana kl. *esculenta* Linnaeus, 1758[3]	2n		Before-meiosis exclusion[15] + endomitosis[16]	Hybridogenesis[18]	*R. ridibunda* *R. lessonae* [9]
	3n	nd , less.[14]	Idem, and ameiosis[17]		*R.* kl. *esculenta*
Unnamed *Rana* klepton	2n	nd , perezi[20]	B-meiosis excl ?	Hybridogenesis[20]	*R. perezi*
Unnamed *Rana* klepton	2n	nd , bergeri[21]	B-meiosis excl. ?	Hybridogenesis[21]	*R bergeri*
Amphibians: *Ambystoma* complexes					
Precedent nomenclature: formal names[22,23] and hyphenated names[24]					
Ambystoma kl *nothagenes* Kraus, 1985	3n[1x],4n[2x]	lat , tex., tigr.[26]	(?)	(?)	*A tigrinum*? *A. laterale*?[25]
Ambystoma kl. *platineum* (Cope, 1867)[2]	2n[24],3n[22,27],4n[24]	lat , jeff[27,28]	Endomitosis[22,29,30,31]	Hybridogenesis[22] Gynogenesis?[22,27,34,30] Parthenogenesis ?[?][15,22,25]	*A tigrinum*? *A. texanum*?[32,36,32] *A jeffersonianum*?[22] *A maculatum*?[16]
Unnamed *Ambystoma* klepton	2n,3n[37,38,32x],4n[36,32]	lat , tex[37,18]	(?)	(?)	*A laterale*? *texanum*?[33]
Unnamed *Ambystoma* klepton	3n[19]	lat., jeff., tigr[39]	(?)	(?)	
Unnamed *Ambystoma* klepton	3n,4n[36,28]	lat., jeff., tex[36,34]	(?)	(?)	

reproductive mechanism (hybridogenesis or gynogenesis). It was the case of *Rana* kl. *esculenta* LINNAEUS, 1758, *Ambystoma* (Cope, 1867), and *Poecilia* kl. *formosa* (GIRARD, 1859). Current authors continue to use those ancient names, and DUBOIS & GÜNTHER (1982) proposed simply to introduce the abbreviation " kl. " in the binomial to distinguish them from species.

Thus the major nomenclatural controversies that now occur concern kleptons that still are unnamed.

Several papers have been published concerning these topics, and the dilemma involves two major alternatives: the use of hyphenated names as proposed by SCHULTZ (1969), and the use of DUBOIS & GÜNTHER's (1982) klepton nomenclature.

Hyphenated nomenclature consists in giving all parental names of genomes composing the hybrid, each one being preceded by a number indicating the ploidy level of each genome (for instance *Ambystoma laterale-(2)jeffersonianum-tigrinum*). This is a genetic systematic point of view.

I choose the klepton nomenclature because I consider that system as most practical from an evolutionary, general biological and phenotypical points of view. The klepton nomenclature lets us treat separately each case with different binomial, just introducing the particle " kl. " between. But it also implies that authors studying different hybridogenetic and gynogenetic hybrid taxa must undertake careful description of all known kleptons. Fully complete description is needed, including morphology. For instance in European complexes of *Rana* there are two quite well genetically known kleptons yet unnamed. That constitutes an additional difficulty for people concerned for their conservation, ecological study and zoogeographical considerations.

In the absence of complete descriptions of kleptic taxa, provisional names could be employed. For instance GRAF & POLLS PELAZ (1989) utilize *Rana* kl. RP (*Rana ridibunda-perezi* sensu SCHULTZ 1969) for referring to one still unnamed Southern Europe hybrid. Either SCHULTZ's hyphenated names or other lettered or numbered nomenclatures could be provisionally accepted until formal kleptic names are substituted, once complete descriptions of those taxa are provided.

WHEN IS A NEW KLEPTON JUSTIFIED ? THE PROBLEM OF POLYPLOIDS

Biological characteristics of *Ambystoma* kl. *nothagenes* KRAUS, 1985, are noted in Table I. I know that Canadian workers on the *Ambystoma* complex disagree with consideration of this taxon as a separate species (BOGART & LICHT, 1986; LOWCOCK et al., 1987). They are correct. It is not a species but a klepton. Kleptic nomenclature and the BKC concept should substitute for the BSC. The case is a classic illustration of conditions justifying the erection of a new klepton.

As a klepton is the result of hybridization between two or more species, all new discoveries of hybrids should be nomenclaturally recognized. Thus the discovery by KRAUS (1985) of triploid hybrids with parental genomes of *Ambystoma laterale*, *A.*

texanum, and *A. tigrinum* was a biological novelty (no other combination of those parental genomes was known before in the *Ambystoma* complex) and the erection of a new name was required and fully justified. A question arises, however, because *Ambystoma* kl. *nothagenes* populations include both triploid and tetraploid gynogenetic and hybridogenetic individuals, just as *Rana* kl. *esculenta* includes diploid, triploid, and diploid-triploid populations.

I propose that all different ploidy combinations with the same parental genomes be included in the same klepton. The main reason is that genetic flow exists between different ploidy forms. For instance diploid *Rana* kl. *esculenta* females in Germany produce both diploid and triploid progeny, thus preventing consideration of diploids and triploids as separate taxa. On the other hand, recent studies of BOGART & LICHT (1986) showed how diploid, triploid, and tetraploid progenies were from the same *Ambystoma* triploid females in Lake Erie. Obviously, separate nomenclature for different ploidy levels would be biologically inacceptable. For these very same reasons I consider *Ambystoma tremblayi* Comeau, 1943 (*Ambystoma 2 laterale-1 jeffersonianum*, sensu SCHULTZ, 1969) a junior synonym of *Ambystoma* kl. *platineum* (Cope, 1867) (*Ambystoma 1 laterale-2 jeffersonianum*, sensu SCHULTZ, 1969) (see Table 1).

KLEPTONS TOWARD THE STATUS OF SPECIES

Kleptons become species either when they become genetically autonomous, or when their hybrid origin is concealed, by accumulative mutations (sensu lato). The phenomena could be compared to diploidization of tetraploid new species after entire genome duplication (OHNO, 1970).

As some peripheral subspecies are involved in speciation processes, thus some kleptic populations could be considered in speciation process, too. Such appears to be the case for some *Rana* kl. *esculenta* populations of East Germany. In these populations *esculenta* hybrids seem to be autonomous with respect to the species *Rana ridibunda* (see a review in GRAF & POLLS PELAZ, 1989). I understand these situations as speciation events (or perhaps only attempts), and I propose to consider these cases as examples of " good " species arising from a kleptic origin (fig. 1).

Perhaps speciation events in *Xenopus* (by allopolyploidy, KOBEL & DU PASQUIER, 1986) are analogous to current hybridogenetic processes in *Rana* kl. *esculenta* (see DUBOIS, 1977). As a matter of fact, derivation of new species from hybrid origin really seems to be related to the tetraploid level (MURAMOTO & OHNO, 1968; OHNO, 1970; COMINGS, 1972; BOGART, 1980; FISHER et al., 1980; ALLENDORF & THORGAARD, 1984). Autotetraploids frequently show tetrads in aberrant meiosis, whereas allotetraploids with an equilibrated parental genome hybrid dosage could constitute a double number of bivalents, and " ordinary " meiosis could happen; therefore mixis of diploid gametes could originate a new gonochoric species of tetraploid hybrid origin. Triploids giving diploid gametes could be an intermediate step between kleptons and species in the *Rana* kl. *esculenta* complex.
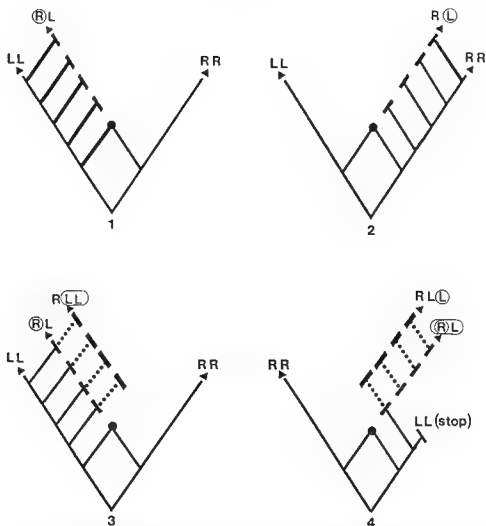
Fig 1 - Some evolutionary trees illustrating different genetical sytems in the Palearctic populations of *Rana* kl *esculenta* complex: 1 (the so-called L-E system), 2 (the so-called R-E system); 3 (all-male allotriploid genealogies in Fontainebleau forest); and 4 (Serrahn pure *esculenta* populations) Circles indicate hemiclonally transmitted genomes Abbreviations refer to the following genomes: R = *R. ridibunda*, L = *R. lessonae*, RL, RLL = *R.* kl. *esculenta*. For more explanations see the review of GRAF & POLLS PELAZ (1989)

INTROGRESSION, MOSAICISM,
AND CLONAL-HEMICLONAL DIVERSITY IN KLEPTONS

Kleptons seem to play an important rôle as a genetic vector of introgression both between their associated " good " species, and between other involved klepton. For instance high introgression levels of *Poeciliopsis viriosa* genes into the *monacha* hybrido-

genesis-inducer genome have been found in Rio Moccorito's *Poeciliopsis monacha-viriosa* hybrid populations. In those populations recombinant *monacha-viriosa* haploid gametes occur, becoming inductors of hybridogenesis when crossed with sympatric individuals of *Poeciliopsis lucida*. Thus diploids of *Poeciliopsis (monacha-viriosa)-lucida* become separate, hemiclonal hybridogenetic taxa in reproductive dependence on the " good " species *P. lucida* (VRIJENHOEK & SCHULTZ, 1974). This unnamed klepton seems to have evolved as a separate unit, perhaps much closer to the species level than Rio Grande triploid kleptons of trihybrid *monacha-viriosa-lucida* genome dosage. I conclude that high levels of introgression should be reflected with the use of separate names. Low levels of introgression (for instance in some populations of *Rana* kl. *esculenta* complex, see a review in GRAF & POLLS PELAZ, 1989) are irrelevant for consideration of separate taxa.

Mosaicism occurs in *Phoxinus* kleptons (DAWLEY & GODDARD, 1988) as well as in some " good " species (SERRA, 1965), and findings of this kind must not be considered problematic for using kleptic nomenclature for hybrids with hybridogenetic or gynogenetic reproduction.

Hemiclonal and clonal diversities in *Rana* and *Poeciliopsis* kleptons have been reviewed respectively by HOTZ (1983) and VRIJENHOEK (1984). This would constitute a problem for nomenclatural systems based only on genome dosage (because each clone is a " separate ", self-evolving genome). But no problem is encountered in kleptic nomenclature, which provides for different degrees of polymorphism between populations.

KLEPTONS AND EVOLUTION

" The species are the real units of evolution. " (MAYR, 1982: 621).

It could be that all genotypes in tetrapod vertebrate taxa have a common ancestor (500 Myr ago) in which duplication at least once of the entire genome took place (OHNO, 1970). In some cases in entire families, as salmonids (ALLENDORF & THORGAARD, 1984) and catostomids (FERRIS, 1984), as well as at least twelve more fish species (ALLENDORF & THORGAARD, 1984), a trace of " recent " (in catostomids 50 Myr) polyploidization events still remains. Polyploid amphibians and reptiles are surprisingly common (DUBOIS, 1977; BOGART, 1980). In some cases, as in the entire genus *Xenopus*, evidence of allopolyploidy remains (KOBEL & DU PASQUIER, 1986). In other case, as for instance in the triploid-tetraploid *Carassius auratus* complex, hybrid origins are likely, because the parental species are allopatric, and divergent evolution of the taxa has taken place (LIEDER, 1955; CHERFAS, 1966; KOBAYASI, 1971; KOBAYASI et al., 1970).

But it is clear that hybridization could be the basis of polyploidy (BOGART & WASSERMAN, 1972; DUBOIS, 1977), perhaps in the way proposed by SCHULTZ (1969), by (1) the origin of a triploid strain (hybridogenetic or gynogenetic, unisexual or not), followed by (2) occasional fertilization of the triploid by normal diploid to produce fertile tetraploids.

Gametogenetic mechanisms are involved. CUELLAR (1987) reviewed all meiosis variants for parthenogenesis (sensu lato, including hybridogenesis and gynogenesis) in plants and animals, in discussing " Spontaneous versus Hybridization controversy " In

fact meiotic, premeiotic, and before-meiosis *extravagancies* (Table I) are at the origin of all gynogenetic and hybridogenetic hybrid populations. I conclude that at least some kleptons could be considered as hybrid taxa currently evolving toward the status of polyploid " good " species. The process could be favored by heterosis (BULGER & SCHULTZ, 1979; MOORE 1976, 1984), and hemiclonal-clonal adaptation of hybrids to intermediate environments (THIBAULT, 1978; THIBAULT & SCHULTZ, 1978).

PERSPECTIVE IN THE USE OF KLEPTIC TERMINOLOGY

The history of taxonomy is an evolutionary event, too, and it is not evident whether kleptic nomenclature will be accepted by the international scientific community. Some European authors routinely use this system of nomenclature for the *Rana* kl. *esculenta* complex. The advanced state of knowledge in *Poeciliopsis*, *Phoxinus* and *Poecilia* complexes seems to be adequate for the full use of kleptic nomenclature, although names are needed for taxa as yet unnamed.

The 1985 *Code* authorizes interpolation   as the proposal for interpolation of " kl. " in scientific names – although to be sure in a different context, viz. species-groups and subspecies-groups. The principle is the same, however, if the insertion of " kl. " is proposed (see the *Code*, Art. b, p. 10, H. M. SMITH, in litteris).

Canadian zoologists working on the *Ambystoma* complex seem to be in mutual accord for the use of hyphenated names. Since knowledge of some unnamed *Ambystoma* taxa is still inadequate (for instance we do not know if parthenogenesis occurs, even after recent papers published by BOGART and colleagues), it seems consistently proper to continue to use provisional terms

It was LINNAEUS who first used binomial names for species. But that concept was erected thousands of years earlier by Grecians such as ARISTOTELES. And the BSC needed around two centuries from LINNAEUS to MAYR in order to become formally constituted. The klepton systematic-evolutionary category was proposed only in 1982 by DUBOIS & GÜNTHER, from which the BKC is available; its fate may require decades to be finalized.

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